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Projection and uncertainty of the poleward range expansion of coral habitats in response to sea surface temperature warming: A multiple climate model study

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Abstract Using projected monthly mean sea surface temperature (SST) in the 21st century obtained by multiple climate models and SST-based indices for the poleward range expansions of three types of coral habitats, we quantitatively evaluated the effects of SST warming on potential northern limit of coral habitats in seas close to Japan and their uncertainty in the global warming projections. The uncertainty in the timing of temperate coral community formation due to global warming was no less than 30 years, with a modulation of ± 10 years due to decadal climate variability. Tropical-subtropical and temperate coral communities and coral occurrence in seas close to Japan were predicted to shift poleward by a few hundred kilometers by the end of the 21st century. The average estimated speeds of the shifts were 1, 2, and 4 km/year for the tropical-subtropical coral community, temperate coral community, and coral occurrence, respectively. The simulated speeds were relatively slower than those previously observed (up to 14 km/year; Yamano et al. 2011), indicating that there are time lags between the new recruitment of coral colonies and the establishment of

coral communities. Hence, monitoring of coral dynamics in response to SST warming is required. Collaboration between monitoring and modeling would enhance the reliability of future projections of changes in coral habitats. Such projections are important for conserving marine biodiversity and developing plans for human societies to adapt to global warming.

Keywords coral habitats, global warming, sea surface temperature, climate models, decadal climate variability, uncertainty

Introduction

Corals play a fundamental role in primary production and habitat formation for numerous other species in tropical and subtropical oceans. Thus, their poleward range expansions due to sea surface temperature (SST) warming can cause fundamental modifications of tem-

perate coastal ecosystems. Recent monitoring data and eyewitness reports have suggested that tropical-subtropical corals in the temperate area of Japan are migrating northward (e.g. Nojima and Okamoto 2008; Nomura et al. 2008; Sugihara et al. 2009; Yamano and Namizaki 2009). On the basis of 80 years of national records for temperate areas in Japan, as well as the studies above, Yamano et al. (2011) showed the first large-scale evidence of the poleward range expansion of modern corals in response to SST warming. They found that the speed of these expansions reached up to 14 km/year, far greater than that for other biological species.

SST warming makes the need to precisely project future changes in coral habitats urgent, not only to conserve marine biodiversity, but also to plan for the adaptation of human societies to the changes. Using the monthly mean SST projected by a high-resolution climate model (K-1 model developers 2004) and SST-based indices of the potential northern limit of coral habitats based on observations, Yara et al. (2009) quantitatively evaluated the potential effects of SST warming on corals in seas close to Japan in the 21st century. They found that the temperature-determined northern limit of tropical-subtropical coral communities, which is currently located in southern Kyushu, should migrate northward to northern Kyushu. They also reported that the northern limit of coral habitats, currently located in Niigata and Chiba prefectures, should move north to Aomori and Iwate prefectures by the end of the 21st century.

While Yara et al. (2009) used the single climate model, multiple climate model projections from the World Climate Research Programme's (WCRP's) phase 3 of Coupled Model Intercomparison Project (CMIP3; Meehl et al. 2007), which performed for the Fourth Assessment Report of the Intergovernmental Panel on Climate Change (IPCC AR4; Solomon et al. 2007), are available. The projected SST warming trends over the North Pacific varied among the CMIP3 models (e.g., Yamaguchi and Noda 2006; Oshima et al. 2012). Therefore, we must pay special attention when evaluating the projected results of the poleward range shifts and/or expansions of coral habitats based on the SST warming trends obtained by the multi models, because some uncertainty exists in the CMIP3 multi-model projections.

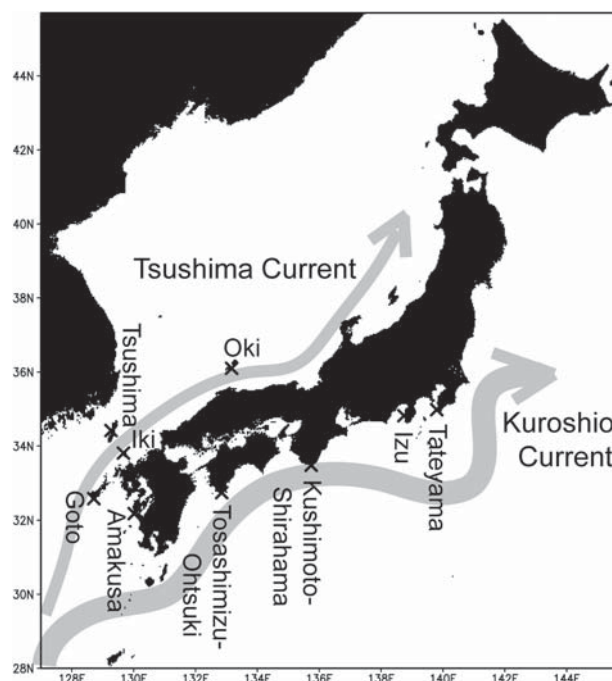


Fig. 1 Nine temperate study regions in seas close to Japan where on-site monitoring of the poleward range expansion of coral habitats has been conducted: Oki (133.2°E, 36.1°N), Iki (129.7°E, 33.8°N), Tsushima (129.3°E, 34.4°N), Goto (128.7°E, 32.6°N), Amakusa (130.0°E, 32.2°N), Tosashimizu-Ohtsuki (132.9°E, 32.8°N), Kushimoto-Shirahama (135.7°E, 33.5°N), Izu (138.8°E, 34.8°N), and Tateyama (139.8°E, 35.0°N). Arrows denote typical positions of the Kuroshio and Tsushima currents

This study quantitatively examines the potential effects of SST warming on the northern limit of coral habitats in seas close to Japan in the 21st century, based on the CMIP3 multi model projections. In addition, we evaluate the timing of poleward range expansions of coral habitats in nine temperate study regions (Fig. 1), as well as the uncertainties resulting from differences in the SST warming trends among the models. The next section describes materials and methods about the SST-based indices for poleward range shifts and/or expansions of coral habitats and the SST datasets from the multiple climate models used in this study. The third section states results and discussion about the projected poleward range expansions of coral habitats and their uncertainties, and the real-world application. The last section mentions conclusions, including considerations when applying modeling results to the real world are suggested to enhance collaboration between

monitoring and modeling.

Materials and methods

SST-based indices for coral habitats

Three SST-based indices, developed and introduced by Yara et al. (2009), describing the potential northern limits of the habitats of three corals are used in this study. Monthly-mean isothermal lines of 18°C, 13°C, and 10°C in the coldest months are defined as the northern limits of the tropical-subtropical coral community (coral assemblage generally associated with reef building), the temperate coral community (coral assemblage composed of several species, generally not associated with reef building), and coral occurrence, respectively.

Previous studies have reported that the global distribution of reef-building corals is limited by annual minimum temperatures of 18°C (e.g. Veron 1995; Kleypas et al. 1999; Buddemeier et al. 2004). Therefore, 18°C may be regarded as the limit of establishment of tropical-subtropical coral communities. About 40 coral species were found with high coverage in the Iki Islands, where the water temperature in the coldest month was 13.3°C (Yamano et al. 2001). Only three species were found in the Oki Islands, where the water temperature was less than 13°C (Sugihara et al. 2009). Therefore, 13°C can be considered the limit of establishment of temperate coral communities. Finally, the northernmost limit of coral occurrence (*Oulastrea crispata*) is Sado-ga-Shima (Niigata Prefecture), where the water temperature is ~10°C (Honma and Kitami 1978).

Datasets of modeled SSTs

Monthly mean SSTs from 23 CMIP3 model projections (Table 1) were used to develop the SST-based indices above. The models have horizontal resolutions ranging from 0.2° to 5°. We employed “the 20th century climate in coupled models” (20C3M) simulations from 1980 to 1999 and the global warming projections under the Special Report on Emissions Scenarios (SRES) A1B scenario, which assumes a future world of rapid economic growth with a balanced emphasis on all energy sources (Solomon et al. 2007).

Table 1 Climate models providing the monthly mean SSTs used in this study and the horizontal resolution of the models

Model	Horizontal resolution
BCCR-BCM2.0 (Norway)	0.5–1.5° × 1.5°
CGCM3.1_T47 (Canada)	1.9° × 1.9°
CGCM3.1_T63 (Canada)	0.9° × 1.4°
CNRM-CM3 (France)	0.5–2° × 2°
CSIRO-MK3.0 (Australia)	0.8° × 1.9°
CSIRO-MK3.5 (Australia)	0.8° × 1.9°
GFDL-CM2.0 (USA)	0.3–1.0° × 1.0°
GFDL-CM2.1 (USA)	0.3–1.0° × 1.0°
GISS-AOM (USA)	3° × 4°
GISS-EH (USA)	2° × 2°
GISS-ER (USA)	4° × 5°
FGOALS-g1.0 (China)	1.0° × 1.0°
INGV-SXG (Italy)	1–2° × 2°
INM-CM3.0 (Russia)	2° × 2.5°
IPSL-CM4 (France)	2° × 2°
MIROC3.2_hires (Japan)	0.2° × 0.3°
MIROC3.2_medres (Japan)	0.5–1.4° × 1.4°
ECHO-G (Germany/Korea)	0.5–2.8° × 2.8°
ECHAM5-MPI-OM (Germany)	1.5° × 1.5°
MRI-CGCM2.3.2 (Japan)	0.5–2.0° × 2.5°
NCAR-PCM1 (USA)	0.5–0.7° × 1.1°
UKMO-HadCM3 (UK)	1.25° × 1.25°
UKMO-HadGEM1 (UK)	0.3–1.0° × 1.0°

Because there are generally biases in climate model results, we corrected biases in the monthly mean SST in each of the CMIP3 models using the procedure introduced by Yara et al. (2009). First, we calculated monthly mean SST anomalies during 2000–2099 (i.e., 1200 months) under the A1B scenario projection relative to the monthly mean climatology (the 20-year mean SST from 1980 to 1999) in the 20C3M simulation. Second, the SST anomaly for each month during 2000–2099 was added to the observed monthly mean climatology (18-year-mean SST from 1982 to 1999) of the National Oceanic and Atmospheric Administration (NOAA) Optical Interpolation Sea Surface Temperature (OISST; Reynolds et al. 2007), interpolated to horizontal grid point in each of the CMIP3 models. Then, we calculated monthly mean SST in coldest month for each year from the bias-corrected SST during

2000–2099. The bias-corrected SST in the coldest months from 2000 to 2099 was used for our evaluation in this study. Because it takes a long time to form coral colonies, we assume the SST mean for each decade in the 21st century as the long-term mean field of the SST. Decadal-mean SSTs were used for the evaluations in this study.

The global warming trend and decadal variability components of the SST in the coldest months obtained by the CMIP3 multi-models were compared to one another and also with monitoring data. The comparison was performed at nine temperate study sites in seas close to Japan (Fig. 1). The coral occurrence surveys were conducted by Nojima (2004), Nomura et al. (2008), Sugihara et al. (2009) and Yamano et al. (2011) at Amakusa (130.0°E, 32.2°N), Goto (128.7°E, 32.6°N), Iki (129.7°E, 33.8°N), Tsushima (129.3°E, 34.4°N), and Oki (133.2°E, 36.1°N) in the East China Sea and Japan Sea, and at Tosashimizu-Ohtsuki (132.9°E, 32.8°N), Kushimoto-Shirahama (135.7°E, 33.5°N), Izu (138.8°E, 34.8°N), and Tateyama (139.8°E, 35.0°N) in the Pacific.

Results and discussion

Projected poleward range expansions of coral habitats and their uncertainties

The projected locations of the northern limits of coral habitats in each decade in the 21st century were evaluated based on the decadal mean SST in the coldest months in the 23 CMIP3 model projections (Fig. 2). The projected results obtained from the CMIP3 multi-models were mostly similar to one another, except in the Pacific Ocean south of Tokyo in 2000s through 2020s. This is because the northern limit of the tropical-subtropical coral community, defined by the monthly-mean isothermal lines of 18°C, was predicted to locate in the south of the Kuroshio Current. In this oceanic region, as the latitudinal gradient of SST is small, a slight difference of the projected SST among the models leads to a large difference in the location of the isothermal lines. The difference among the models decreases after 2030s when the northern limit shifts to the north of the Kuroshio Current in which the latitudinal gradient of SST is relatively large. Because different models project different responses to the same external forcing as a result of their treatments of physical

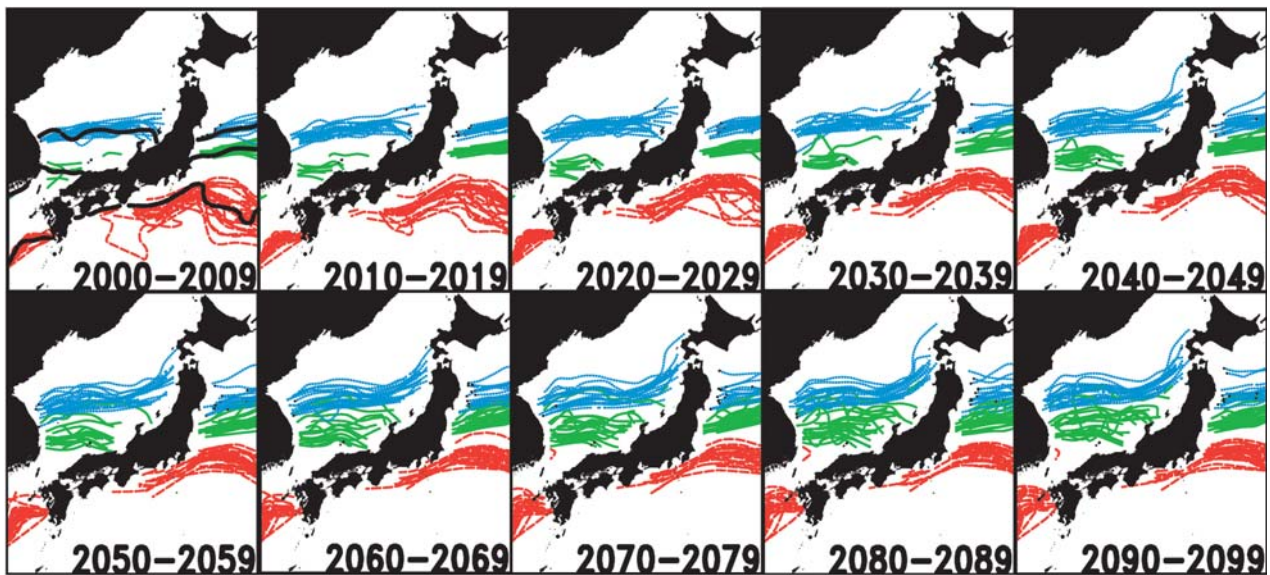


Fig. 2 Projected 10-year mean northern limit of tropical-subtropical coral communities (red lines), temperate coral communities (green lines), and coral occurrence (blue lines) in seas close to Japan from 2000 to 2099 obtained by multiple climate models. The black lines in the figure for 2000 to 2009 denote the 10-year mean observed monthly-mean isothermal lines of 18°C, 13°C, and 10°C in the coldest months estimated by the NOAA OISST

processes, numerical schemes, and other factors, different regional patterns and magnitudes of the SST warming trends were projected in the CMIP3 models, leading to uncertainties in the model projections.

Two factors contribute to the uncertainties in the decadal mean SST in climate model projection under a single scenario (e.g. Deser et al. 2010; Hawkins et al. 2009; Oshima et al. 2012). The first factor is the difference in SST warming trends among the CMIP3 models. The second factor is the phase of the decadal variability. The ocean-atmosphere climate system has intrinsic variability on decadal time scales due to effects such as the Pacific Decadal Oscillation. The phase of the decadal SST variability contributes to the decadal-mean SST, but this phase cannot be predicted in the CMIP3 model projections. To evaluate the uncertainties from these two factors quantitatively, we divided the temporal variability of the SST in the coldest months in the 21st century into three components: the global warming trend ($\Delta\text{SST}_{\text{gw}}$), the

decadal variability (ΔSST_d), and the interannual variability (ΔSST_i). The latter was shorter than the decadal variability and was analyzed. Then, the SST was expressed as the sum of the SST climatology (SST_c) and the three temporal components as follows:

$$\text{SST} = \text{SST}_c + \Delta\text{SST}_{\text{gw}} + \Delta\text{SST}_d + \Delta\text{SST}_i. \quad (1)$$

In this study, the $\Delta\text{SST}_{\text{gw}}$ was calculated from the linear trend of the monthly mean SST in the coldest months from 2000 to 2099. The ΔSST_d was defined as a 5-year running mean component of $(\text{SST} - \text{SST}_c - \Delta\text{SST}_{\text{gw}})$. The residue $(\text{SST} - \text{SST}_c - \Delta\text{SST}_{\text{gw}} - \Delta\text{SST}_d)$ was defined as the ΔSST_i . The ΔSST_i was relatively small, and most of the variability cancels out in the decadal mean. Therefore, the ΔSST_i is regarded as noise in the following discussions of the uncertainty. To evaluate the range of the uncertainty from the decadal variability, we calculated the standard deviation of ΔSST_d ($\Delta\text{SST}_d(\text{SD})$ hereafter; Fig. 3). The $\text{SST}_c + \Delta\text{SST}_{\text{gw}} + \Delta\text{SST}_d(\text{SD})$ and $\text{SST}_c + \Delta\text{SST}_{\text{gw}} - \Delta\text{SST}_d(\text{SD})$

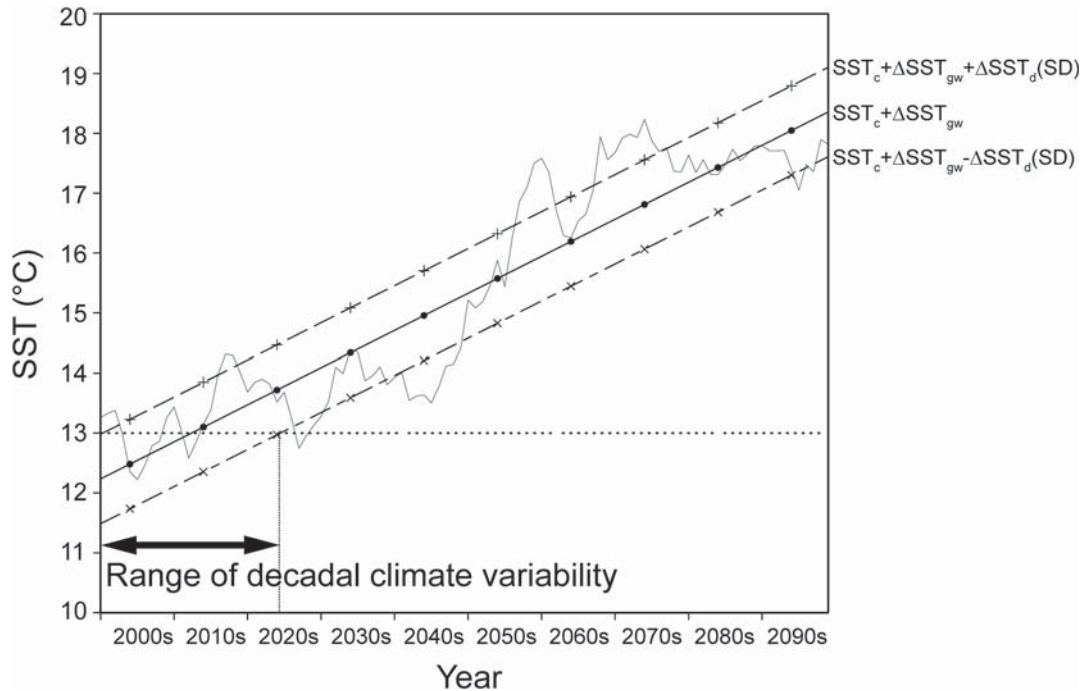


Fig. 3 Schematic diagram of the decadal climate variability in the SST discussed in this study. The thin solid line, thick solid line, thick dashed line, and thick chained line denote the projected monthly mean SST, $\text{SST}_c + \Delta\text{SST}_{\text{gw}}$, $\text{SST}_c + \Delta\text{SST}_{\text{gw}} + \Delta\text{SST}_d(\text{SD})$, and $\text{SST}_c + \Delta\text{SST}_{\text{gw}} - \Delta\text{SST}_d(\text{SD})$, respectively, in the coldest months in the 21st century. The $\Delta\text{SST}_d(\text{SD})$ is defined as the standard deviation of ΔSST_d . The range of decadal climate variability is defined as the difference in timing of temperate coral community formation at the site after the $\text{SST}_c + \Delta\text{SST}_{\text{gw}}$ in the coldest months exceeds 13°C (shown as a thin dotted line), between the $\text{SST}_c + \Delta\text{SST}_{\text{gw}} + \Delta\text{SST}_d(\text{SD})$ and $\text{SST}_c + \Delta\text{SST}_{\text{gw}} - \Delta\text{SST}_d(\text{SD})$ cases

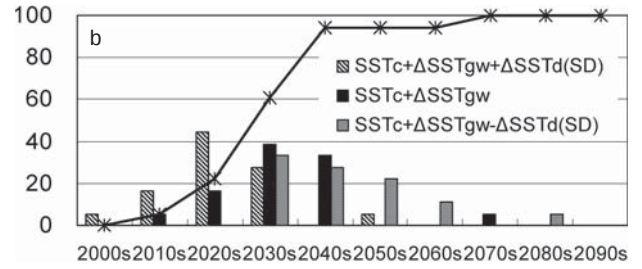
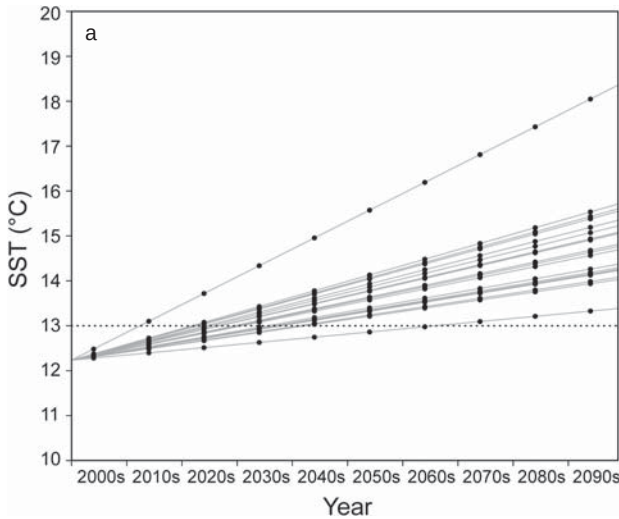


Fig. 4 **a** Projected global warming trend of the monthly mean SST ($SST_c + \Delta SST_{gw}$) in the coldest months in Oki from 2000 to 2099, obtained from multiple climate models. The temperate coral community was assumed to be formed at this site after the $SST_c + \Delta SST_{gw}$ in the coldest months exceeded 13°C (shown as dotted line). **b** Probability (%) of temperate coral community formation in Oki for the $SST_c + \Delta SST_{gw} + \Delta SST_d(\text{SD})$, $SST_c + \Delta SST_{gw}$, and $SST_c + \Delta SST_{gw} - \Delta SST_d(\text{SD})$ cases (bars) and the cumulative probability (%) of the $SST_c + \Delta SST_{gw}$ case (line) from the 2000s through 2090s projected by the multiple climate models

(SD) cases were defined as positive and negative phases of the decadal variability, respectively. The range of the two cases indicates a difference in the timing; i.e., the uncertainty due to the decadal variability as to when coral communities will form in a site after $SST_c + \Delta SST_{gw}$ in the coldest months exceeds 18°C (for tropical-subtropical coral community), 13°C (for temperate coral community), or 10°C (for coral occurrence). The original monthly mean SST was within the range of the two cases in most years, with some exceptions. For example, monthly mean SST was occasionally lower than $SST_c + \Delta SST_{gw} - \Delta SST_d(\text{SD})$ in the 2040s and higher than $SST_c + \Delta SST_{gw} - \Delta SST_d(\text{SD})$ in the 2050s through 2070s, when it was affected by ΔSST_d , which is regarded as noise.

The uncertainties in the projected effects of SST warming on the poleward range expansion of coral habitats in Oki were assessed using $SST_c + \Delta SST_{gw}$ in the coldest months in the CMIP3 multi-model projections (Fig. 4a). Although the magnitude of the warming trend varied among the models, the median timing of temperate coral community formation (defined by the arrival of the monthly-mean isothermal line of 13°C in the coldest months) was the 2030s, and most (16 out of 18) models predicted that the timing was between the 2020s and 2040s at this site (Fig. 4b). The timing could be modified by around ± 10 years by the decadal variability that each

climate model has as the natural variability. Combining the uncertainties from differences in the warming trends and in the decadal variability among the models, we predicted the timing of temperate coral community formation at this site to be 2030s ± 10 years, modified by the decadal variability. We used the SST of the climate model grid point closest to Oki. However, the grid points were not sufficiently close to Oki if the climate model had relatively coarse horizontal resolution. Therefore, we had to analyze the SST in each model independently.

In the nine temperate study regions described above, Oki was the only station that was located north of the temperate coral community limit (defined as the monthly-mean isothermal line of 13°C in the coldest months). The projected probability of the start of tropical-subtropical coral community formation at the stations from the 2000s to 2090s is shown in Fig. 5 and defined as the arrival of the monthly-mean isothermal line of 18°C in the coldest months. Although the projected results were substantially different because of uncertainties in the warming trend and decadal variability, it is unlikely that tropical-subtropical coral communities will form in Oki, Tsushima, Iki, Goto, Tateyama, and Izu within the 21st century. Seas close to Amakusa will be covered with tropical-subtropical coral communities by the end of the 21st century.

Real-world applications

Most climate models predicted that the northern limits of tropical-subtropical coral community, temperate coral community, and coral occurrence, which are located in southern Kyushu, Shimane and Ibaraki prefectures, and Niigata and Chiba prefectures in the first decade of the 21st century, will shift northward by a few hundred kilometers to northern Kyushu, Ishikawa and Fukushima prefectures, and Aomori and Iwate prefectures, respectively, by the last decade of the 21st century. The average speed of the expansions obtained by the models is 1, 2 and 4 km/year for the tropical-subtropical coral community, temperate coral community, and coral occurrence, respectively. The speed varies by the species, reflecting regional difference in the SST warming trends among the models (Oshima et al. 2012). Coral occurrence is fastest, while the tropical-subtropical coral communities are slowest.

The estimated speeds are smaller than the speeds of recent expansions reported by Yamano et al. (2011). The speeds for tropical-subtropical coral community expansion were generally smaller than those of the tropical species (*Acropora hyacinthus* and *Acropora muricata*; 0–14 km/year). The speeds for temperate coral community expansion were also smaller than those of more temperate species (*Acropora solitaryensis* and *Pavona decussata*; 2–8 km/year).

The discrepancy in the speed of the coral community expansions between this study and Yamano et al. (2011) is presumably caused by two reasons. One is resulting from a difference in classification of coral species. In this study, corals were classified into three communities, and the average speed of each coral community expansion that has a time scale of ~ 10 years is discussed. In Yamano et al. (2011), on the other hand, the speed of the new recruitment of several colonies of specific indicator species was detected. Another reason includes the difference of environmental changes that were taken into account between this study and Yamano et al. (2011). In this study, SST warming is the only factor that drives the poleward range expansion of coral habitats while in reality there are multiple factors such as water depth, light condition (e.g. Kleypas et al. 1999), salinity, abrupt (day-week time

scale) drop of temperatures in winter (e.g. Burns 1985; Hoegh-Guldberg et al. 2005), nutrient concentration, and competition with large seaweeds.

Future works should consider possible influences of driving factors besides SST warming such as mentioned above that may affect coral communities. While this study demonstrates the possibility of the poleward range expansion of coral habitats in response to SST warming in subtropical and temperate regions, the SST warming is expected to intensify both frequency and area of coral bleaching or death in lower latitude regions such as the Ryukyu Islands (Yara et al. 2009). Future increases in ocean acidification may counteract the poleward range expansion of coral habitats. Recent studies have suggested that ocean acidification and the subsequent decrease in carbonate ion concentration may hamper the calcification of coral skeletons, especially at higher latitudes, which have lower SSTs and lower carbonate ion concentrations (e.g. Kleypas et al. 1999; Guinotte et al. 2003; Orr et al. 2005; Hoegh-Guldberg et al. 2007).

Ocean current patterns are another important factor for considering the poleward range expansions of coral habitats because the ocean currents transport coral eggs and larvae. On the other hand, we need to pay special attention that previous modeling studies suggest an increase in the velocity of the Kuroshio and Kuroshio Extension (Sakamoto et al. 2005) and a northward shift of the Kuroshio Extension (Sato et al. 2006) in response to global warming, indicating the different results with models.

Conclusions

Using the projected monthly mean SST in the 21st century obtained by the 23 CMIP3 climate models and SST-based indices for poleward range expansion of coral habitats, we examined the effects of SST changes due to global warming and decadal variability on potential northern limit of coral habitats in seas close to Japan and discussed the uncertainties in the global warming projections. Combining the uncertainties from differences in the warming trends and in the decadal variability among the models, we predicted the timing of temperate coral

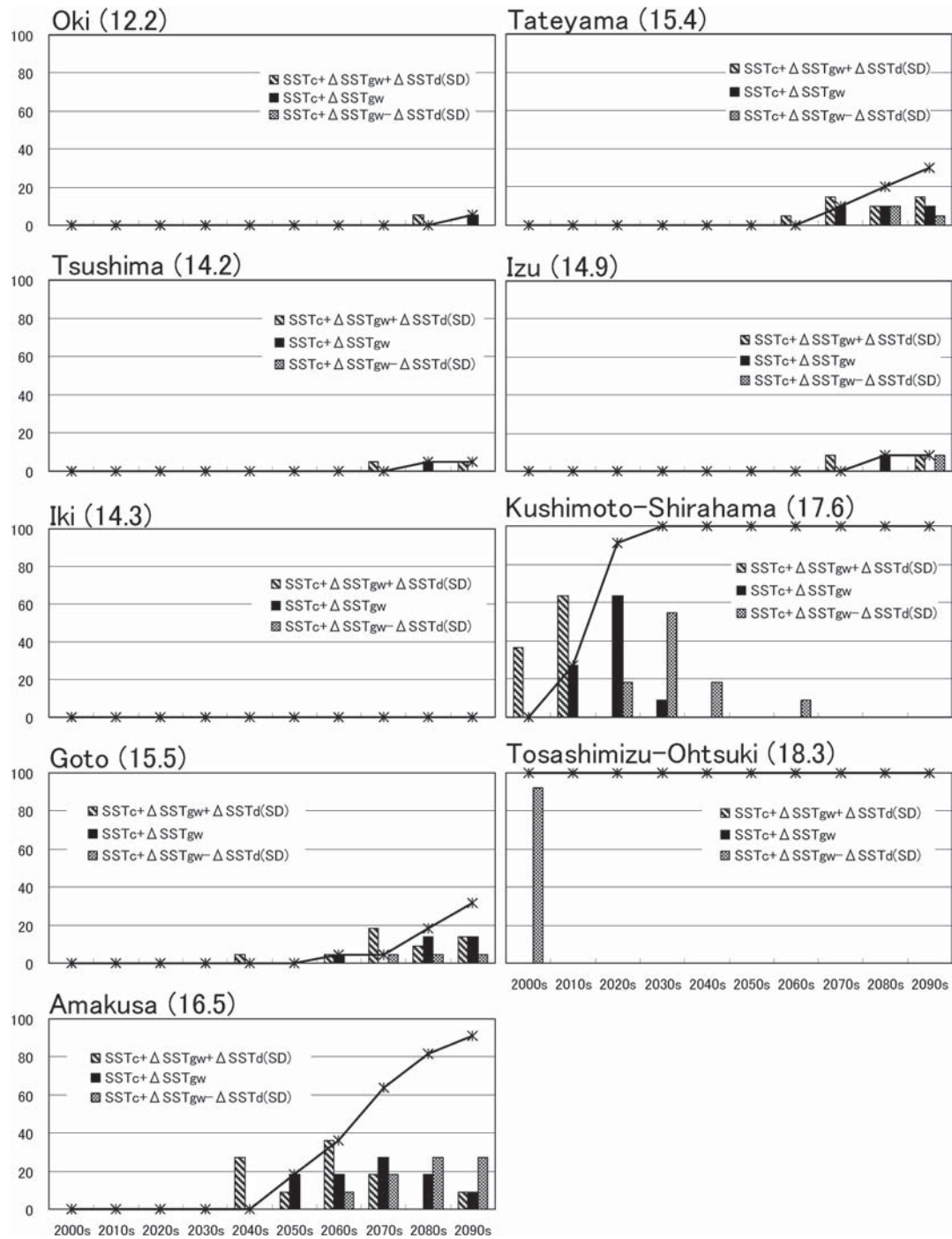


Fig. 5 Probability (%) of tropical-subtropical coral community formation in nine temperate study regions for the $SST_c + \Delta SST_{gw} + \Delta SST_d(SD)$, $SST_c + \Delta SST_{gw}$, and $SST_c + \Delta SST_{gw} - \Delta SST_d(SD)$ cases (bars), and cumulative probability (%) of the $SST_c + \Delta SST_{gw}$ case (line) from the 2000s through the 2090s projected by the climate models. Numbers in parentheses indicate average *in situ* SST minima (°C) of the coldest months

community formation in Oki to be 2030s ± 10 years, modified by the decadal variability. The simulated results suggest that tropical-subtropical and temperate coral communities and coral occurrence in seas close to Japan will shift poleward by a few hundred kilometers by the end of the 21st century. The average speeds of the shifts are estimated to be 1, 2, and 4 km/year for tropical-subtropical coral communities, temperate coral communities, and coral occurrence, respectively. These speeds are relatively smaller than the speed of 14 km/year based on 80 years of observed records (Yamano et al. 2011).

The uncertainties in the simulated results are considerable. Some uncertainties arise from differences in greenhouse gas emission scenarios and the models' spatial resolution and sensitivity to climate. These uncertainties can be alleviated by future model improvements. In contrast, the uncertainty caused by the natural variation derived from the internal variability in each model cannot be removed. However, we estimated the temporal range of the decadal climate variability in each coral habitat formation to be 20 years. We may need to validate climate models through comparisons of multi-model results along with long-term monitoring data to minimize the underlying uncertainties.

Both uncertainties in the predictions and the dynamics of corals require long-term monitoring to reveal the dynamics from new recruitment of colonies and establishment of communities in response to SST warming, especially for specific indicator species such as *Acropora hyacinthus*, *Acropora muricata*, *Acropora solitaryensis*, and *Pavona decussata* defined by Yamano et al. (2011). Collaboration between monitoring and modeling would enhance the reliability of future projections of changes in coral habitats and provide a baseline for designing future strategies for local industries such as fisheries and tourism to adapt to global warming.

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